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DEVELOPMENT OF THE MEGAGAMETOPHYTE
IN LIQUIDAMBAR STYRACIFLUA L.

FRANKLIN F. FLINT

No work has been published on the megagametophyte of *Liquidambar*. Within the family (Hamamelidaceae) only two other genera have been studied in regard to megasporogenesis and megagametogenesis (Flint, 1957, 1957A).

Pistillate floral heads of *Liquidambar styraciflua* were collected in Dinwiddie County, Virginia, from March 28 until July 10, 1953. They were fixed in formalin-aceto-alcohol in the proportions of 90 cc. of 70 percent ethyl alcohol to 5 cc. formalin and 5 cc. of glacial acetic acid. Tertiary butyl alcohol, as used by Johansen (1940), was found most satisfactory for dehydration. The heads were then embedded in tisseumat, sectioned at 10-30 microns, and stained with Harris' Hemotaxylin, Safranin O, and Fast Green FCF.

Around 245 ovules are included in this study. Ovules which showed signs of unusual plasmolysis, nuclear degeneration, or had unusually dark staining cytoplasm were eliminated and are not included in the above count.

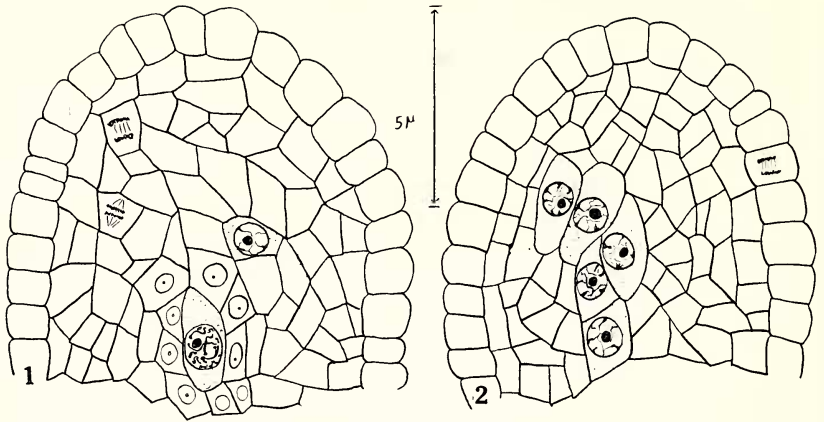


FIG. 1. Young ovule with one megaspore mother cell and one other enlarged nucellar cell. FIG. 2. Young ovule with five potential mother cells. Only one will form megaspores.

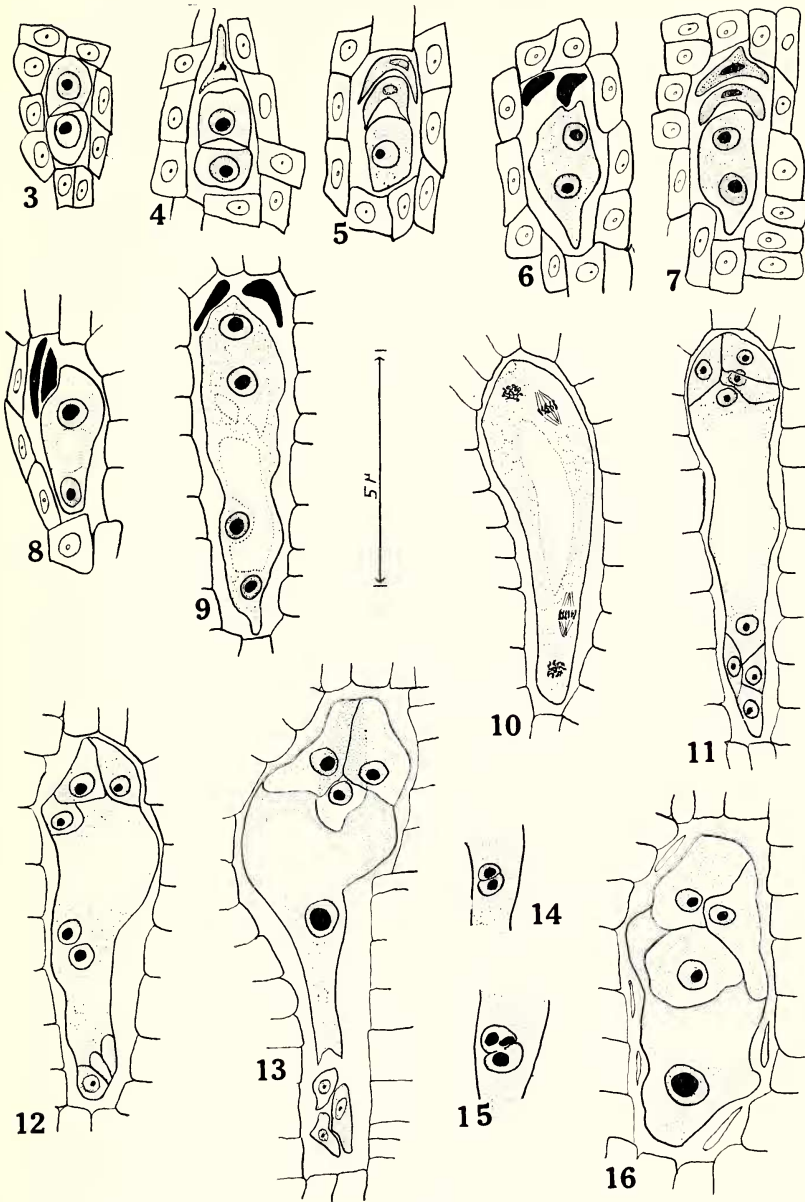
MEGASPOROGENESIS

The ovules are formed in two rows within each locule and develop from its base toward the apex. As many as twelve to eighteen ovules are initiated in each locule although only two to six usually form gametophytes and these are most often located near the base of the locule. The ovules may cease development and become degenerate during any stage of megasporogenesis or megagametogenesis.

The megaspore mother cell is first distinguishable within the young ovule, embedded beneath seven to nine layers of nucellar cells. This cell is large, nearly oval in shape, with dense cytoplasm, and a large vesicular nucleus (fig. 1). Frequently as many as five large cells are present within the nucellus and have the appearance of megaspore mother cells (fig. 2). Only one of these cells in an ovule undergoes the meiotic divisions, and it is then that the functional megaspore mother cell can first be determined. In such ovules the functional mother cell is most often located near the center of the group of enlarged cells. After meiosis I is completed, cytokinesis takes place, and a dyad of cells of approximately the same size, each with dense cytoplasm and a large, deeply staining nucleus containing a prominent nucleolus, is formed (fig. 3). The chalazal dyad cell completes meiosis II and cytokinesis takes place, but the micropylar dyad

FIGS. 3-5. Megasporogenesis. 3, dyad cells formed from meiosis I of megaspore mother cell; 4, micropylar dyad cell disintegrating while chalazal dyad cell undergoes meiosis II and forms two megaspores; 5, enlarging chalazal megaspore with upper megaspore and micropylar dyad cell disintegrating.

FIGS. 6-16. Megagametogenesis. 6, young 2-nucleate megagametophyte; 7, beginning of vacuoles in 2-nucleate megagametophyte; 8, vacuoles have coalesced in center



of 2-nucleate megagametophyte; 9, 4-nucleate megagametophyte; 10, nuclear divisions to form 8-nucleate megagametophyte; 11, egg apparatus formed, also antipodals, but before migration of polar nuclei; 12, polar nuclei have migrated to center of megagametophyte; 13, polar nuclei have fused and antipodals are disintegrating; 14, fusion of two polar nuclei; 15, fusion of two polar nuclei and sperm nucleus; 16, enlarged egg apparatus of mature megagametophyte.

cell degenerates without undergoing this division (fig. 4). The linear triad of cells which results from this activity consists of the degenerating micropylar dyad cell and the two megaspores formed by the chalazal dyad cell (fig. 4). In all cases observed the chalazal megaspore enlarged further and became the only functional megaspore (fig. 5). The other two cells of the triad are soon pushed aside by the developing megagametophyte which presses them against the surrounding nucellar cells where they gradually disintegrate (figs. 5, 6, 7, 8, 9).

MEGAGAMETOGENESIS

In the ovules studied the chalazal megaspore increases in size, the nucleus divides, and gradually a 2-nucleate megagametophyte is formed (fig. 6). As the cell continues to enlarge, two small lateral vacuoles appear in the cytoplasm, one to either side of the nuclei (fig. 7). Growth of the megagametophyte continues and the two lateral vacuoles coalesce into a single large central vacuole as one of the nuclei and part of the cytoplasm move toward the micropylar end and the other nucleus and remainder of the cytoplasm move toward the chalazal end of the cell (fig. 8). Rapid growth of the megagametophyte continues and each of the nuclei undergoes another division forming a 4-nucleate cell with a pair of nuclei at either end oriented along the major axis of the megagametophyte (fig. 9). The four nuclei undergo a division with one spindle at each end of the megagametophyte oriented along the major axis of the cell and one spindle at each end oriented perpendicular to the major axis (fig. 10). This division results in an 8-nucleate megagametophyte with four nuclei located at either end. The megagametophyte elongates further and the egg apparatus, consisting of three cells, is soon formed at the micropylar end of the megagametophyte (fig. 11). There is no discernible differentiation into an egg cell and two synergids at this time. Three distinct, comparatively large, antipodal cells are formed at the chalazal end of the megagametophyte (fig. 11). The two polar nuclei, one located beneath the egg apparatus and the other directly above the antipodal cells, are immersed in thin cytoplasm and separated by a central vacuole. The polar nuclei soon migrate toward the center of the megagametophyte and lie next to each other (fig. 12). The antipodal cells begin to degenerate (fig. 12) and then separate from each other and the primary endosperm cell (fig. 13). At the same time the micropylar end, containing the egg apparatus, increases in size (fig. 13). The egg cell is soon distinguished from the two synergids by its larger nucleus (fig. 16). The polar nuclei may fuse to form a secondary nucleus (fig. 14) or fusion may be delayed until the sperm nucleus enters, in which case all three nuclei fuse at once to form the primary endosperm nucleus (fig. 15). With the disintegration of the antipodal cells the megagametophyte becomes broader, the single secondary nucleus (or the primary endosperm nucleus, as the case may be) and the egg apparatus enlarge (fig. 16). The cytoplasm of the two synergid

cells becomes vacuolated and a small vacuole often appears above the egg nucleus within the greatly enlarged egg cell.

SUMMARY

The megaspore mother cell is embedded beneath seven to nine nucellar cell layers. There are frequently more than one and sometimes as many as five large cells which resemble megaspore mother cells in a single ovule, but only one of these cells functions. A linear triad of cells is formed as the chalazal dyad cell undergoes meiosis II and the micropylar dyad cell does not. In previously studied species of the Hamamelidaceae only one potential megaspore mother cell forms in each ovule and both dyad cells undergo meiosis II to form a linear tetrad of megaspores. The chalazal megaspore develops into the megagametophyte in all species studied. The pattern of development is essentially that of the *Polygonum* type listed by Maheshwari (1950).

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REVIEWS

A Flora of San Francisco, California. By JOHN THOMAS HOWELL, PETER H. RAVEN, AND PETER RUBTZOFF. 157 pp., 20 figs., 1 map. The Wasmann Journal of Biology, Vol. 16, No. 1. 1958. Published in book form by the University of San Francisco. Paper. \$3.00.

In spite of the many people now living within the city limits of San Francisco, an amazing number of native plants are still to be found. This is largely due to the hilliness of the city. The hilltops, bluffs, and cliffs provide refuges, many of which have not as yet been commercially exploited. Some habitats, notably the marshes and sand dunes, are rapidly disappearing. On Bernal Heights, however, *Dodecatheon patulum* var. *bernalinum* still grows at its type locality and *Aristolochia californica* is still to be found in ravines near Lake Merced.

In 1892, Katharine Brandegee listed 605 taxa of vascular plants in her "Catalogue of the Flowering Plants and Ferns Growing Spontaneously in the City of San Francisco." Howell, Raven, and Rubtzoff list 1132 species, subspecies, varieties, forms, and hybrids as growing spontaneously in San Francisco now or in the past. Of these, about 42 per cent are introduced plants and about 19 per cent have not been collected since 1940 and are probably now extinct locally. A number of garden escapes are included. Among them are: *Pseudosasa japonica*, *Pittosporum crassifolium*, 2 species of *Cotoneaster*, 3 species of *Acacia*, *Albizzia lophantha*, *Cassia tomentosa*, *Ruta chalepensis*, and *Buddleia davidii*. The main criterion used for inclusion of a particular garden escape is "whether or not the plant could survive in San Francisco without